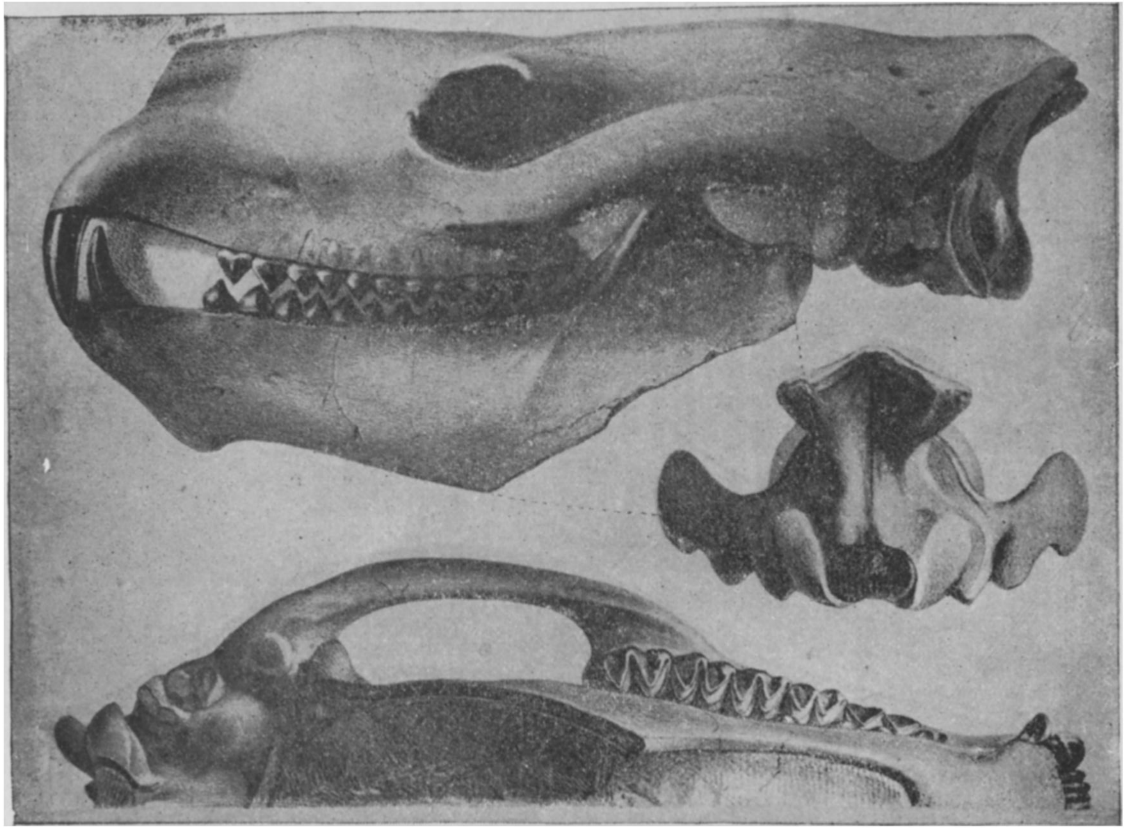
PLATE III.



Agriochoerus guyotianus Cope.

THE ARTIODACTYLA.

BY E. D. COPE.

(Continued from page 1095, Vol. XXII., 1888.)

IN passing from the lower to the higher Artiodactyla we encounter a succession of modifications of the skeleton which give the suborder a higher specialization than any other among mammals. These may be considered under three heads: First, the consolidation of the bones of the carpus and tarsus; second, the development of a tongue and groove of the humero-cubital and metapodio-phalangeal articulations; and third, increased complexity of the intervertebral articulations.

Of consolidation of the bones of the feet we have first, the coössification of the larger two elements of the distal row of the carpus and tarsus; viz.; the trapezoides and magnum in the former, and the meso- and ectocuneiform in the latter. This commences in the Oreodontidæ (Scott) and continues throughout the succeeding families. The next modification of this kind is the coössification of the cuboid bone with the navicular. This commences with the Tragulidæ, and continues throughout the remaining families. The fusion of the metapodials into cannon bones first appears in geological time in the Tragulidae, as does also the fusion of the ulna and radius (in Hypertragulus), and also in the contemporary Poëbrotheriidæ. The reduction in the number of the digits progresses with varying correlation with the other changes, from five in Oreodon to two in Camelus and Bos. As already explained, similar reductions took place in the Eocene members of the suborder, Anoplotherium having the digits 3-3, and Xiphodon 2-2.

The mechanical cause of these coössifications must be regarded as strains incurred in the act of rapid locomotion. Where not sufficient to produce actual flexure, strain is met by resistance and increased nutrition of the tissue, resulting in a strengthening of material at the point of resistance. With such coössifications comes increased mechanical effective-

ness. Kowalevsky has shown that with the reduction of the number of the digits, the metapodials of those which remain, have increased in transverse diameter, so as to articulate with two distal elements of the carpus and tarsus each,

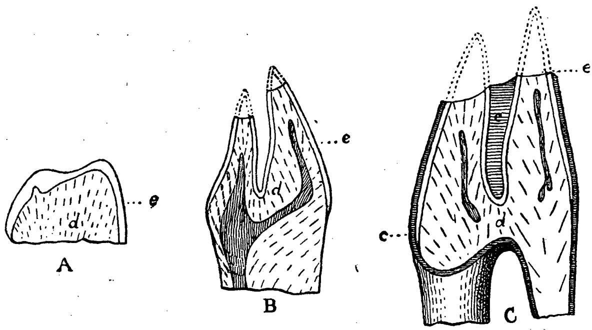


Fig. 7. Transverse sections of molars of Artiodactyla, showing successive complications of structure. A. *Sus erymanthius;* B. *Ovis amaltheus;* C. *Bos taurus;* from Gaudry, Enchainements. Letters: *c*, cementum; *e*, enamel; *d*, dentine.

instead of with but one, as in the primitive types, as Anoplotherium, Hyopotamus and Hippopotamus. (Fig. 8.) He shows that where this expansion of the metapodials did not

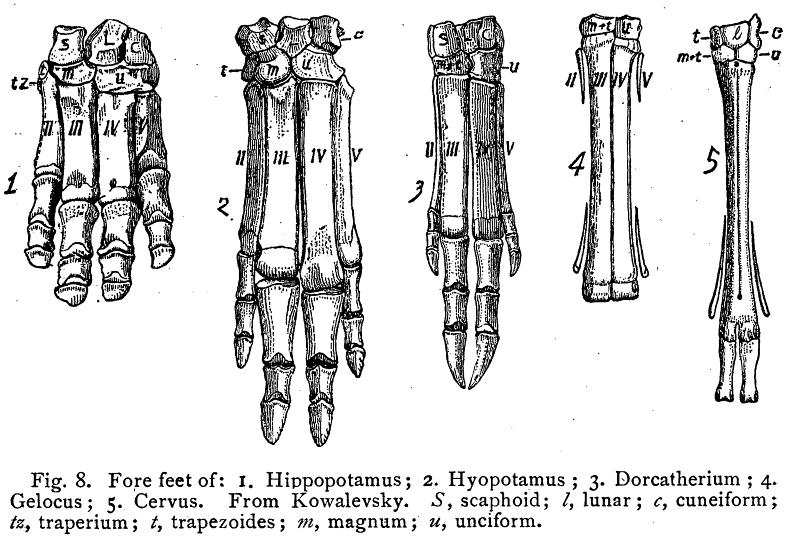
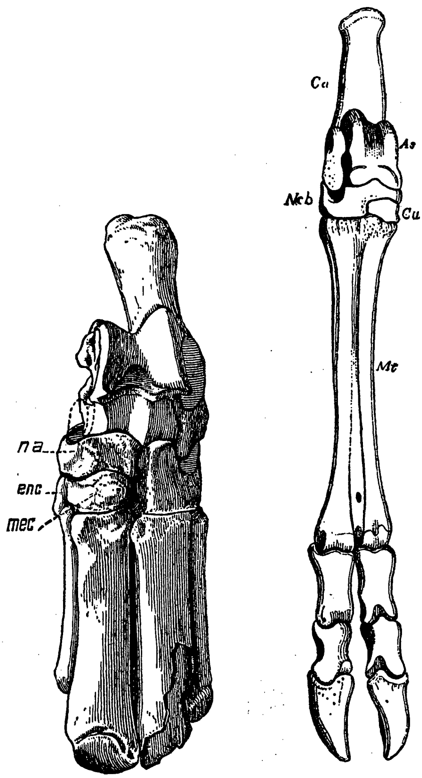


Fig. 8. Fore feet of: 1. Hippopotamus; 2. Hyopotamus; 3. Dorcatherium; 4. Gelocus; 5. Cervus. From Kowalevsky. *S*, scaphoid; *l*, lunar; *c*, cuneiform; *tz*, traperium; *t*, trapezoides; *m*, magnum; *u*, unciform.

take place, the type became extinct, as in Elotherium. He supposes that the extinction of such types was due to the feebleness of the latter construction, which precluded the attainment of any considerable speed on the part of its possessor. The types in which this expansion took place persisted, and became the ancestors of the existing forms. As an example, see Procamelus. (Fig. 10.)



A. B.

Fig. 9. Pes of Artiodactyla. A. *Merycochoerus montanus* Cope, two-fifths natural size. B. *Bos taurus*. L. one-fourth natural size.

The specialization of the elbow joint first becomes pronounced in the Artiodactyla in the Tragulidae. This consists in the development of the external part of the condyles of the humerus into a roller of contracted diameters, and separated from the remaining part of the condyles by a keel, or tongue. The roller and tongue work into a corresponding plane and groove of the head of the radius, forming an interlocking joint of great strength. The strength of the union between the radius and the ulna is increased by the development of a keel on the inferior side of the head of the former, which fits a groove on the upper side of the latter. Both of these structures can be traced from their beginnings in the Artiodactyla. (Plate V.)

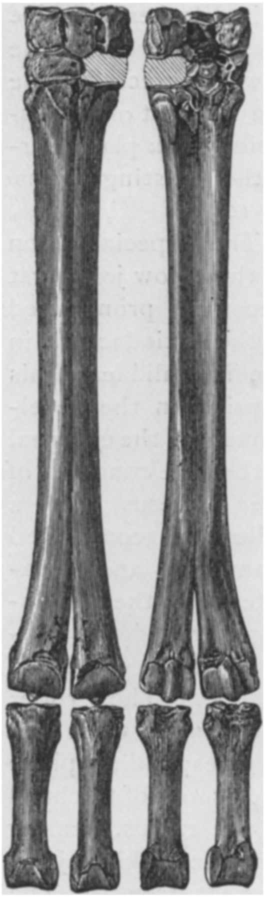


Fig. 10.

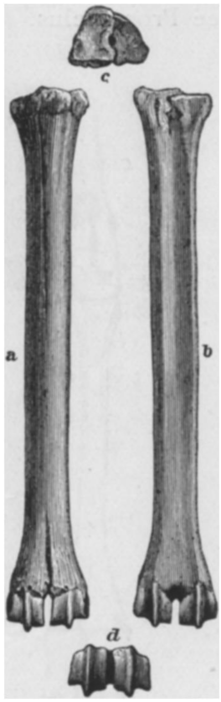


Fig. 11.

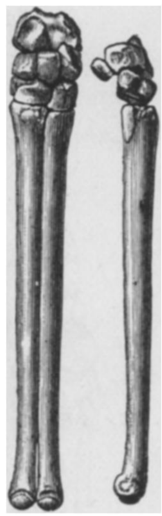


Fig. 12.

Fig. 10.—Part of anterior foot of *Procamelus occidentalis* from New Mexico. From Report of of Capt. G. M. Wheeler, Vol. IV, Pt. II.

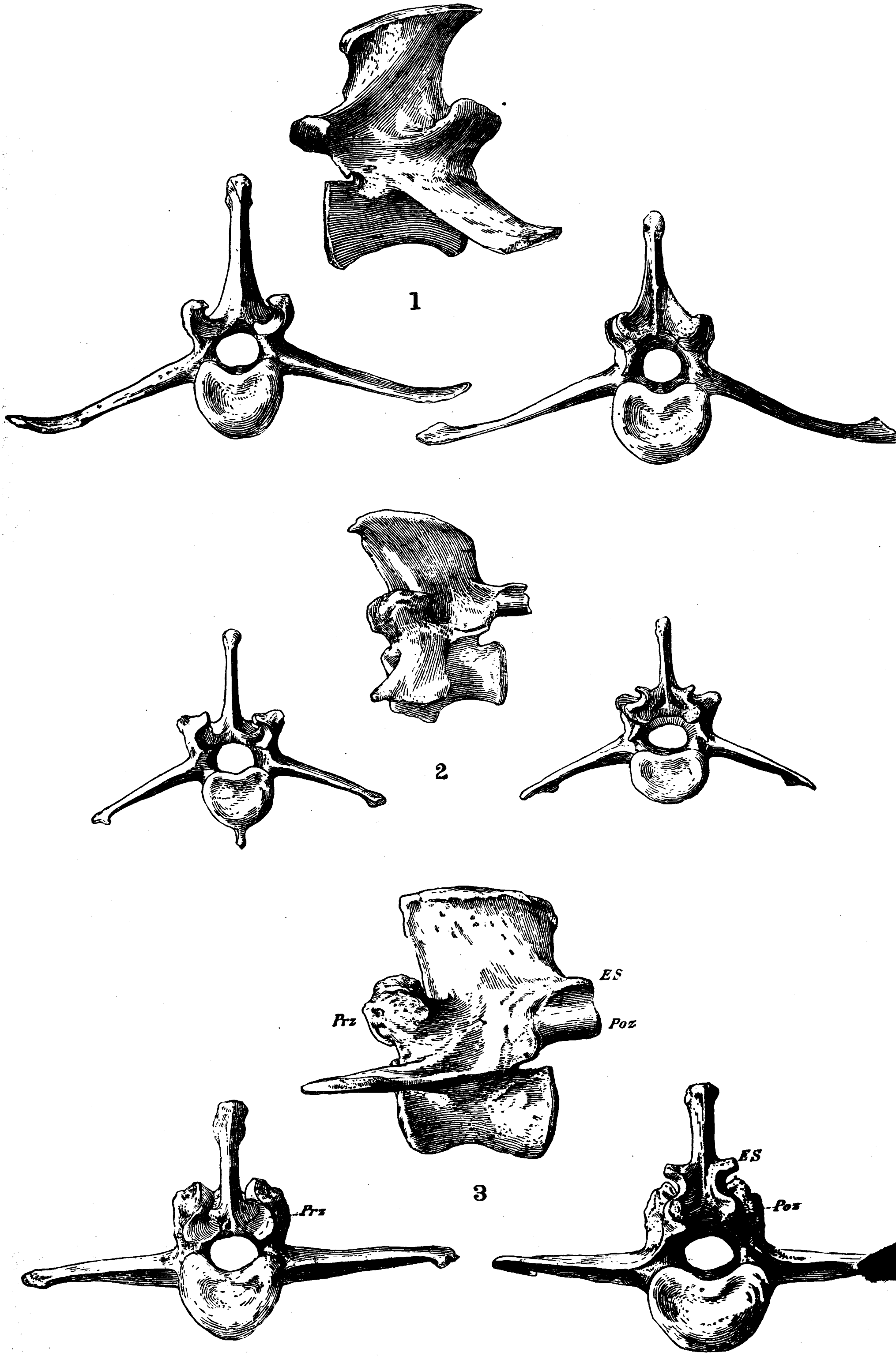
Fig. 11.—Metacarpals of *Cosoryx furcatus* from Nebraska, two thirds natural size; *a*, anterior face; *b*, posterior; *c*, proximal end; *d*, distal end.

Fig. 12.—Left forefoot with part of radius of *Poebrotherium vilsoni* Leidy, from Colorado, three-fifths natural size. From Hayden's report (unpublished).

The trochlear keel or crest,[1] as the tongue of the humerus may be called, is first represented by a convexity of the roller, precisely as in the unguiculate

[1] The trochlear crest of the Artiodactyla is not homologous with the inter-trochlear crest of the Anthropomorpha.

PLATE IV.



Vertebræ of 1, Antilocapra; 2, Dicotyles; 3, Capra.

mammals. (Plate IV. figs. A, D, Hyæna, Eucrotaphus.) With the compression of the external part of the condyle, the external slope becomes steeper and is at length nearly vertical (Ibid, fig. E, Cervus). The mechanical cause of this trochlear crest is the use of a single fore leg to support the body in rapid locomotion. As had been remarked by H. Allen, a modern Artiodactyle in rapid motion lights on one forefoot, which strikes the earth immediately on or even beyond a point below the middle of the body (fig. 13). This throws the impact principally on the external side of the humeral condyles, with the result stated. A similar cause produces a similiar result in the development of the tongue and groove articulation between the metapodials and first phalanges. In lighting on a didactyle foot, the toes are naturally spread, the result being to throw both the first phalanges away from the median line, or axis of impact, in divergent directions. The result of this impact is to produce on each metapodial condyle as in the case of the humerus, an external roller of smaller diameter than the rest of the condyle (fig. 11), and separated from it by an abrupt crest. In both humerus and metapodial bones these crests are accentuated by a pinching process during flexion and extension. This is produced by the longitudinal torsion which results in all limbs in motion from the arrest of the outward rotation of the foot by the earth, on alighting. The

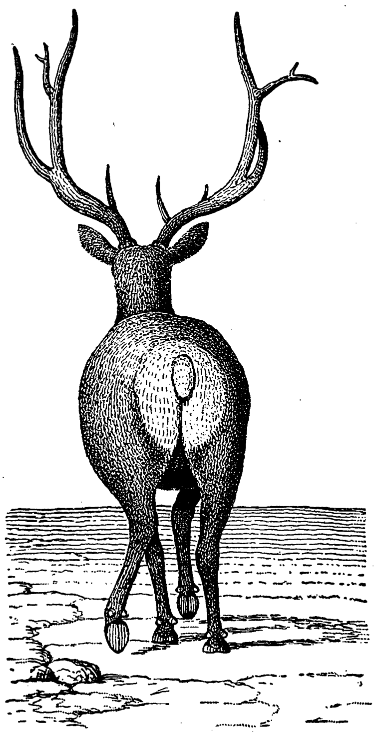


FIG. 13—*Cervus canadensis* in motion, from behind. From the Muybridge photographs.

pinching of a keel by its groove takes place at all points in the length of the former reached by the opposite sides of the extremities of the latter during flexion and extension (fig. 14). This keel becomes acute and prominent in the Boöidea, and extends to the anterior face of the condyle fig. 11, *Cosoryx furcatus*). This development has been apparently especially due to the presence of two sesamoid bones, embedded in the flexor tendons, one on each side of the middle line of the posterior side of the metapodial condyle. The fissure between these bones has permitted the moulding of the surface into a keel to fit it. That this has been the case is further indicated by the fact that a single median trochlear surface exists at the distal extremity of the first phalange in all mammals. But a single flexor tendon crosses

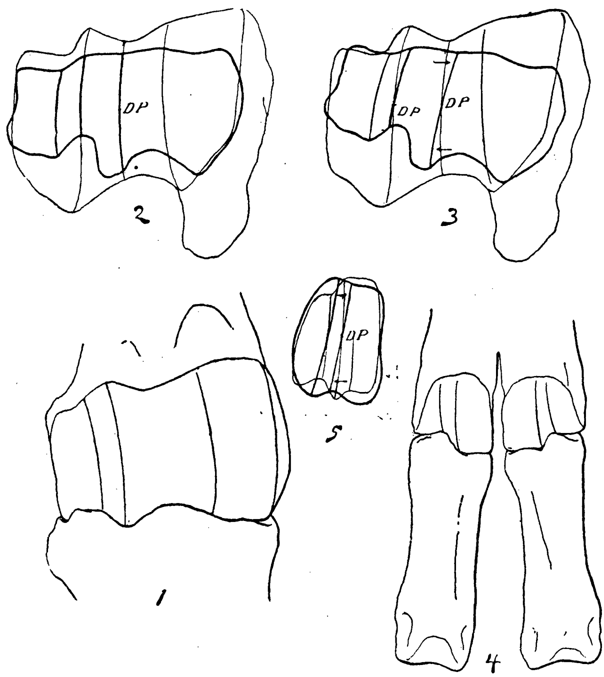


FIG. 14—Tongue and groove joints in *Cervus elaphus*. 1–3, elbow joint with trochlear keel and groove. 1–2, in place; 3, radius dislocated by external torsion. 4–5, metatarso-phalangeal articulation; 4, in place; 5, dislocated by torsion of phalange; *D P*, the dead or fixed point.

this articulation, and it contains but one sesamoid bone, to which the trochlear surface is moulded in a concave surface, as in the case of the patella and the rotular groove of the femur (figs. 8, 9B, 9, 10, 14).

The increased complexity of the intervertebral articulations,[1] is seen in the modifications in the shapes of the zygapophyses.[2] In reptiles the mutual articulating surfaces of these processes are horizontal and flat. In the lower Mammalia they are slightly oblique. In many Carnivora the obliquity is strongly marked, and a similar form is seen in the lower

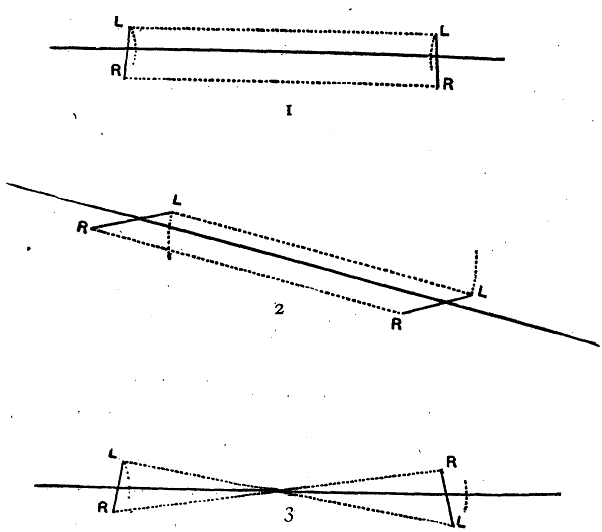


FIG. 15—Diagrams representing movements of the vertebral column in locomotion. 1. The pace; 2. the run; 3. the trot.

Diplarthra. As we ascend the scale of the latter, the prezygapophyses become involute and embrace the postzygapophyses above, as well as externally below (Plate IV., fig. 1, Antilocapra). This superior part of the prezygapophyses develops, and reaches the basis of the neural spine, with which it forms an articulation. The base of the spine expands

[1] For a tabular exhibit of these, see Proceedings Amer. Ass. Adv. Science, 1883; Origin of the Fittest, 1885.

[2] On torsion in locomotion. See art. Perissodactyla, NATURALIST, 1888, 988, 1073.

above this articulation, forming a second process above the postzygapophysis, the episphen. This occurs in the Suoidea and the Boöidea (Plate IV., figs. 2 and 3, Dicotyles and Capra).

The mechanical explanation of the origin of this structure is probably found in the nature of the movement of that part of the vertebral column which is between the limbs during progression; and especially of the more flexible region (lumbar) which is posterior to the ribs. All the gaits of quadrupeds may be reduced to three types, and their varieties. In the first, the extremities of the column are alternately elevated and depressed, without lateral motion. This is seen in the run. In the second, the sides of the column are alternately elevated and depressed. This is seen when the limbs of one side move simultaneously, as in the pace. In the third type, limbs of opposite sides of opposite extremities, move together, as in the walk and trot. The effect of this movement is to twist the column in its long axis. These effects are diagrammatically represented in the accompanying figure 15. It is this torsion which has produced the involuted zygapophyses, and later the episphen. It should be the fact that animals which display this structure should walk and trot, while others should pace and run. And this is the case. The trot as a habitual gait is especially characteristic of the Diplarthra. The Proboscidia and Carnivora pace, although the dogs frequently trot as well. We must suppose that the trot was the favorite gait of the Creodonta, since they possess the involuted zygapophyses.

The only genus certainly referable to the DICHODONTIDÆ, is the Dichodon Owen, from the upper Eocene of England. In this form we have the earliest quadriselenodont molars, the intermediate fifth crescent having disappeared The first superior premolar is like a true molar, while the first inferior is trilobate (Kowalevsky; molariform, Owen). The other premolars are very elongate and compressed, resembling those of Xiphodon. This resemblance is heightened by the incisiform shape of the canines, and the uninterrupted dental series. In the same beds occur limb and foot bones which probably belong to Dichodon (Schlosser) which are didactyle, but in

which the fusion of the trapezoides and magnum in the tarsus, has not yet taken place. The metapodials then rest on a single carpal or tarsal bone each, instead of on two, as in modern didactyle genera, representing the inadaptive type of Kowalevsky. *Dichodon cuspidatus* is about the size of a fallow-deer. Smaller species have been found in Germany. The genus is probably represented in North America by Stibarus Cope, of the White River bed. I have associated provisionally with the Dichodontidæ two North American genera, Agriochoerus Leidy (Plate III.), and Coloreodon Cope (fig. 5). These genera differ from Dichodon in having the first premolars in both jaws molariform or nearly so, and in having the other ones much less compressed, except the fourth inferior, which is caniniform, as in Oreodon. There are four premolars and little or no diastema in Agriochoerus, and three premolars and a long diastema in Coloredon. The former possesses six species, which are equally divided between the White River and John Day beds, and the latter, two species from the John Day Miocene. Their feet are unknown.

The remaining families of the Cameloidea are the Poëbrotheriidæ, Protolabididæ, Camelidæ and Eschatiidæ. I have already described their characters in the pages of the NATURALIST.[1] I will only add to that account the interesting discovery made by Profs. Scott and Osborn, of a third genus of Poëbrotheriidae which they call Leptotragulus. It differs from Poëbrotherium and Gomphotherium, in the separate condition of the ulna and radius.[2] It is from the highest Eocene beds of Utah (Brown's Park, or Uinta system), and thus stands in ancestral relation to Poëbrotherium.

The Cameloid phylum presents a noteworthy peculiarity. The Poëbrotheriidæ have acute trihedral ungual phalanges like those of most other Artiodactyla. In the Camelidæ, including the extinct genus Procamelus, the ungual phalanges are short and obtuse, and apparently undergoing atrophy. This form is associated with the presence of a cushion of connective tissue on the inferior side of the phalanges, which

[1] 1886, p. 611: The Phylogeny of the Camelidæ.

[2] My knowledge of this genus is entirely derived from the unpublished mss. of Profs. Scott and Osborn.

supports the weight of the animal, thus removing it from the ungues. This cushion has relieved the metapodials from impacts and torsion, a fact which I have regarded as explaining the absence of the trochlear keel from the extremity and front of those elements in the Camelidæ. We must then suppose that the development of the elastic foot-pad of the camels began in the Miocene period before this character appears, and caused a divergence from the Booid line in the foot structure. This divergence probably took place before the development of the third stomach, and the addition of water compartments in the paunch may be supposed to have commenced at about the same time.

Existing Camelidæ pace, yet they have more or less distinct episphenal processes to the vertebræ. These are distinctly visible in Procamelus. We must suppose that their ancestors, as the Poëbrotheriidæ, were trotters, and that the habit has been changed in later periods.

With the TRAGULIDÆ we commence the great, mostly modern division of the Boöidea, or Ruminantia. As already related, most of the characteristic peculiarities of the specialized Artiodactyla commence with this family. The trochlear cylinder and crest of the humerus appear here for the first time, for the Suoid and Cameloid series never develop more than traces of either. The naviculocuboid bone is characteristic. How variable the conditions of the other bones of the limbs are in the Tragulidæ may be gathered from the accompanying table. A few species of two genera, Dorcatherium and Tragulus, still exist in the warm parts of Africa and Asia. These agree with the Camelidæ in the absence of the third stomach, the other three being present.

I. Both metatarsals and metacarpals distinct; molars brachyodont (Hypertragulinæ).

a. Lateral toes behind.

Anterior internal cresent of inferior molars represented by a conical cusp. .... *Lophiomeryx* Pom.

Interior cresents of inferior molars developed .... *Dorcatherium* Kaup.

aa. No lateral toes behind.

Diastemata in both iaws .... *Hypertragulus* Cope.

II. Metatarsals forming a cannon bone; metacarpals distinct; molars brachyodont (Gelocinæ).

a. Lateral digits of the manus, none of the pes.

Superior premolars with a small internal tubercle.............. *Leptomeryx* Leidy.

aa. No lateral digits.

Four lower premolars.. *Gelocus* Aym.

Three lower premolars............ .... *Bachitherium* Filhol.

III. A metatarsal cannon bone; metacarpals forming a cannon bone; molars brachyodont (Tragulinæ).

a. Lateral digits well developed.

Premolars entirely simple.................................... *Tragulus* Briss.

aa. Lateral digits weak.

Four inferior premolars, the posterior with branch ridges; superior premolar 3 with strong cingulum........................ *Amphitragulus* Pomel.

Three inferior premolars, the posterior with branch ridges; superior premolar 3 with strong cingulum, elongate.... .... *Prodremotherium* Filhol.

IV. Metatarsals and metacarpals unknown; molars hypsodont (Hypisodontinæ).

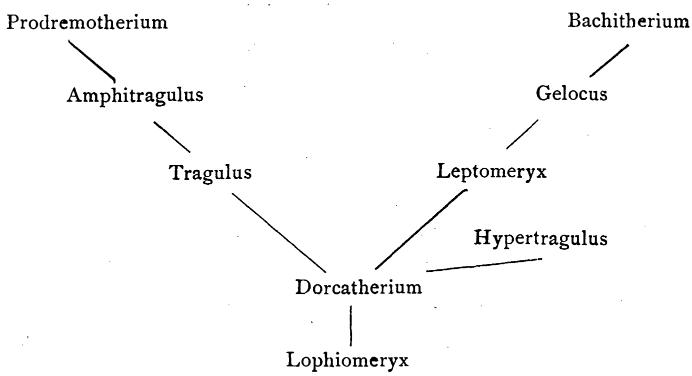
A diastema behind p. m. 2: canines below not distinct from incisors. .... *Hypisodus* Cope.

Dorcatherium, an existing genus, has four well developed digits, and is nearest the Oreodontidæ. The only difference between that family and the present one being the presence and absence of the naviculocuboid bone respectively, Dorcatherium must be placed on the Traguloid side of the line. Probably extinct genera will be found which will connect this genus more intimately with the Oreodontidæ, for the slight complication of the premolars of extinct genera of the latter, testify to earlier members with simpler ones.

Lophiomeryx and Hypertragulus must be associated with Dorcatherium on account of the lack of cannon bone. Lophiomeryx has an inferior type of inferior true molar, and like Dorcatherium has four toes on all the feet. Hypertragulus displays greater specialization in the absence of lateral digits from the posterior feet. The ulna is also coössified with the radius, and there is a naviculocuboid bone. The premolar teeth are nevertheless very simple, and are separated by diastemata in both jaws. It must be regarded as a modified descendant of Dorcatherium on one side of the main line of descent. (Plate VI.)

In the next group the metatarsals have united while the metacarpals remain separate. This is the case in Leptomeryx of the American Oligocene. In Tragulus the premolars are much simpler than those of the other genera of Section III,

and simpler than those of Leptomeryx, so that these two forms must have been derived from an ancestor which combined the simplicity of both forms. For this we must again recur to Dorcatherium, and I therefore insert this genus at the base of the following diagram. With its entirely prismatic molars Hypisodus has one element of superiority, but the number of its superior premolars is unknown.

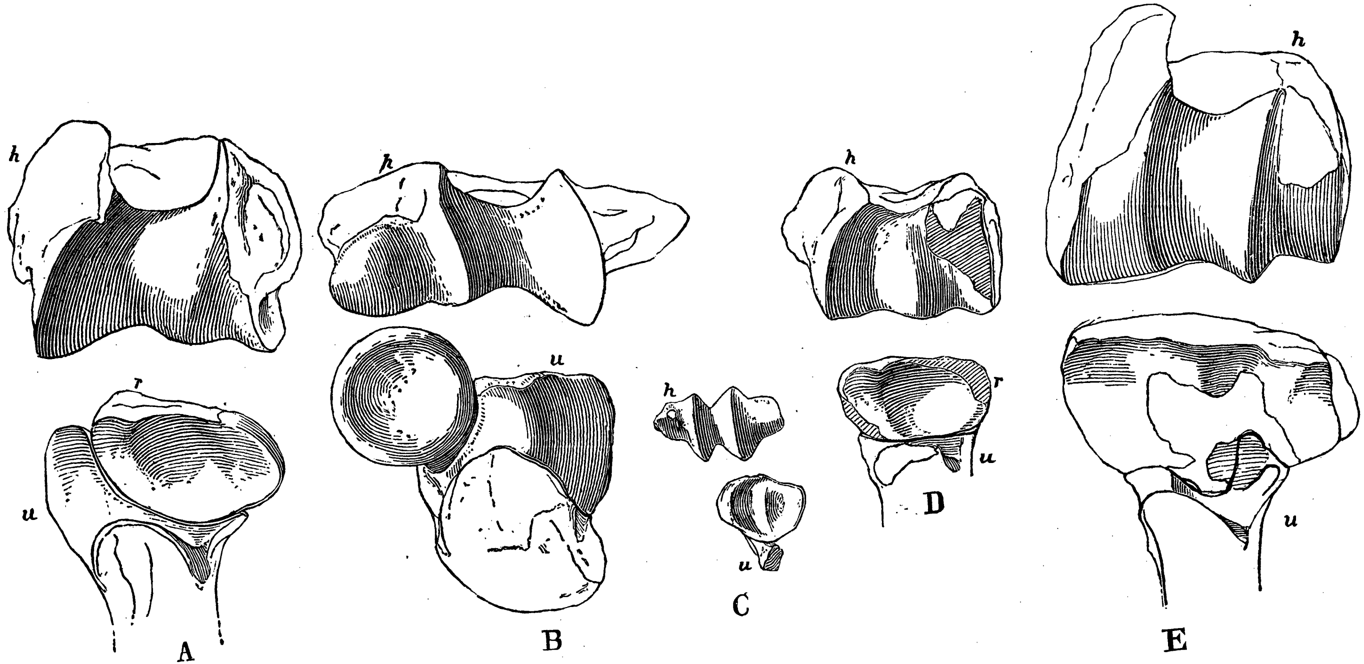


Two species of this family are very abundant in the Cænozoic beds of North America. These are the *Leptomeryx evansi* Leidy of the White River series, and the *Hypertragulus calcaratus* Cope of the same, and of the John Day Miocene series. Either species was of the size of a spaniel, and had delicately formed limbs. The *H. calcaratus* had large eyes, and a compressed muzzle. Larger species are found in Canadian beds. The least species of the family belongs also to the White River Beds. This is the *Hypisodus minimus* Cope, whose size does not exceed that of a gray-squirrel. Like the Leptomeryx, it does not extend upwards into the John Day beds.

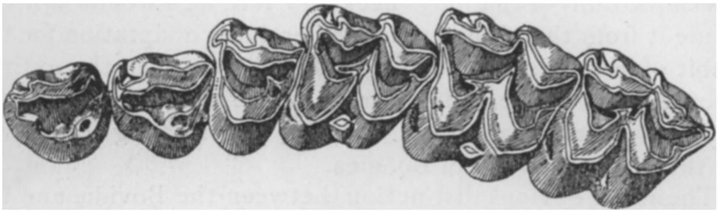
The remaining families of the Boöidea agree in possessing the following characters.

The second and generally the third superior premolar teeth possess an internal crest as well as the fourth fig. 16). The inferior premolar teeth have oblique transverse crests. The keel of the distal extremity of the metapodial bones extends to the front of the condyle (fig. 11). The lateral metapodials are represented by their extremities only, the middle

PLATE V.



Elbow joints of A, Hyæna; B, Simia; C, Rhinolophus; D, Eucrotaphus; E, Cervus.



(FIG. 16.) *Blastomeryx borealis*, Cope, superior molars natural size. From Ticholeptus bed of Montana. Original.

portion having disappeared (fig. 8–5). The median pair are united into a cannon bone. There are no superior incisors. The odontoid process of the axis vertebra is trough-shaped. The stomach is divided into four parts.

The lowest family of the series is that of the Moschidæ. In its hard parts it differs from the Bovidæ in the simplicity of the anterior third superior premolar, which is without the internal crescent found in the other Boöidea. In this respect it is intermediate between that division and the Cameloidea, where the first premolar only possesses the internal crescent. But two genera of Moschidæ are known, Dremotherium from the Lower Miocene of France, and the living Moschus. Both lack horns and have well developed canine teeth. The origin of this group is clearly from the Tragulidæ, and the genus of that family which approaches nearest to it is Amphitragulus, which indeed only differs from it in dentition in the imperfection of the internal crest of the second superior premolar. In turn, Dremotherium must be regarded as ancestral to Palæomeryx, the most primitive genus of the Bovidæ.

The Giraffidæ differ (see table of families) in the mode of attachment of the horns. These are originally separate from the skull, but become attached to it like the epiphyses on the extremities of the bones of the skeleton. Their dental characters are like those of the Cervidæ and the lower Bovidæ, the molars being short crowned or brachyodont. It may be that the condition of the horns in Giraffa represents the mode of origin of the horns of the Bovidæ,[1] and that the genus is simply to be reckoned a primitive type in that family. The

[1] In the sheep the horns begin as bodies separate from the skull.

specialization of the long neck and fore legs would not exclude it from that family. It is merely an adaptation for the habit of browsing on the foliage of tall trees. In the extinct species of its single genus, Giraffa, these characters are found in a less degree than in the existing one, forming transitions to the ordinary forms of Boöidea.

The most obvious distinction between the Bovidæ and the Cervidæ is in the differing character of the bony processes of the skull, used for offense and defense. But where horns are wanting, as is the case with some genera, these distinctions fall to the ground. The horn-type of the Bovidæ is more primitive than that of the Cervidæ, since the horny process is permanent in the former, and is shed and reproduced annually in the latter. The dental type is, however, never so specialized in the deer as is the case with the highest genera of Bovidæ, remaining always distinctly rooted, while in Bos and some other genera of the latter they become prismatic. But the lower genera of Bovidæ do not differ from Cervidæ in this respect.

In accordance with these facts the bovine ruminants appear a little before the cervine, though authors generally refer the earliest genera to the latter division. Such are the genera Dicrocerus and Cosoryx,[1] which appear in the latest Miocene beds. Dicrocerus only differs from Palæomeryx in the possession of horns, which resemble those of deer, but which were, according to Schlosser, never shed, a fact which compels its location in the Bovidæ. In Cosoryx the horns have the same character in this respect, but the teeth are antelopine, or prismatic. It is clearly to be placed in the Bovidæ with Antilocapra (the prong horn,) and it is closely allied to Dicrocerus. Here we see that the point of origin of the two families was from a common ancestor, and that this ancestor was, as has been already expressed by Schlosser, the genus Palæomeryx. Nearly related to this point of departure are the Sivatherium, Bramatherium, and Hydaspidotherium. As they did not shed their horns, they cannot be referred to the Cervidæ. In their covering with the integument, Cosoryx probably possessed a character of Giraffa, which is a primitive

[1] Leidy, Cope; Procervulus Gaudry.

(FIG. 17.) *Dicrocerus furcatus*, posterior part of skull, one-fourth natural size. Miocene, France. From Gaudry.

stage of the essential character of the horns of the Bovidæ. Perhaps the retention of the primitive dermal character of this investment, instead of its metamorphosis into horn, might be regarded as a basis for a distinct family, the Cosorycidæ. But it is highly improbable that this covering remained in Sivatherium and Bramatherium, whose horns were apparently perfectly naked. It is not evident how all these animals can be retained as distinct from the Bovidæ, and I therefore place them in two subfamilies of that family. The Cosorycinæ, which will include Cosoryx and Blastomeryx, are characterized by the sheath of the horns being dermal ; the Sivatheriinæ by the absence of any sheath whatever. The synopsis of genera will then be as follows :

I. No horns in the male.

Molars brachyodont................................... *Palæomeryx*[1] Von Meyer.

II. Horns covered with skin (Cosorycinæ).

Teeth brachyodont ; no frontal excrescence.................. *Blastomeryx* Cope.

Teeth prismatic ; no frontal excrescence...................... *Cosoryx* Leidy.

III. Horns naked (Sivatheriinæ).

Teeth brachyodont ; two pairs of horns, all separate..... *Sivatherium* Cautl. Falc.

Teeth brachyodont ; two pairs of horns ; those of the anterior pair from a common base................................. *Bramatherium* Cautl. Falc.

Teeth brachyodont ; one pair of horns, from distinct bases....... *Dicrocerus* Lart.

IV. Horns covered with a horny sheath ; teeth hypsodont (Bovinæ).

a. No internal column of true molars.

β. No lateral ungues. (Nasal bones normal ; postzygapophyses single).

Horn-sheath furcate .... *Antilocapra* Ord.

Horn-sheath simple.. *Nanotragus* Sund.

[1] Should *P. eminens*, type of Palæomeryx, have possessed horns, as suspected by Schlosser, the generic name must take the place of Dicrocerus below, and be replaced by one of the various names which apply to hornless species.

$\beta\beta$. Lateral ungues present.

γ. Nasal bones separated from maxillary and lachrymal bones.

Horns simple, one pair..*Sæga* Gray.

$\gamma\gamma$. Nasal bones more or less in contact with lachrymal or maxillary bones.

δ. Lumbar postzygapophyses single. (Numerous species not examined)

ε. Inferior premolars three.

Horns one pair..*Antidorcas* Gray.

$\varepsilon\varepsilon$. Inferior premolars four.

Horns two pair..*Tetracerus* H. Smith.

Horns one pair; last inferior molar with four columns..........*Neotragus*[1] Gray.

Horns one pair; last inferior molar with five columns............*Ovis*[2] H. Smith.

$\delta\delta$. Lumbar postzygapophyses double.

Horns one pair; inf. mol. 3 with five columns.....................*Capra* Linn.

aa. One or more superior true molars with a median internal column.

Lumbar postzygapophyses single.............................*Ægocerus* H. Sm.

Lumbar postzygapophyses double...............................*Bos*.[4] Linn.

A great number of names have been given to groups of species of the Bovinæ, especially within the limits of the genus Ovis of H. Smith. Here the various forms of sheep and antelopes have been distinguished as genera, and named accordingly. So far as concerns the skeleton, further subdivisions than those indicated in the above table do not appear to exist, and none have been pointed out. The divisions proposed appear to be rather those of one extensive genus. The modifications of the skull have reference to the position of the horns. These are processes of the frontal bones, and are placed at points from above the eye to the posterior angle of the facial plane of the skull. In the latter case this angle approaches very near to the supraoccipital crest or inion, and the parietal bone is reduced to an exceedingly narrow band between the frontal and occipital bones (Rütimeyer).[5] Forms with anterior horns and well developed parietal bones are *Ovis gazella* and *Tetracerus quadricornis*; while the *Ovis gnu*

[1] *N. saltianus* type. This character is derived from authority to which I cannot now refer. I have not seen it.

[2] Includes the following supposed genera: Antilope, Gazella, Cervicapra, Oreotragus, Cephalophus, Strepsicerus, Damalis, Alcelaphus, Nemorrhædus, Rapicapra, Caloblepas, Haplocerus, Ovis, and Anoa.

[3] Includes the following supposed genera: Eleotragus, Ægocerus, Oryx, Addax and Portax.

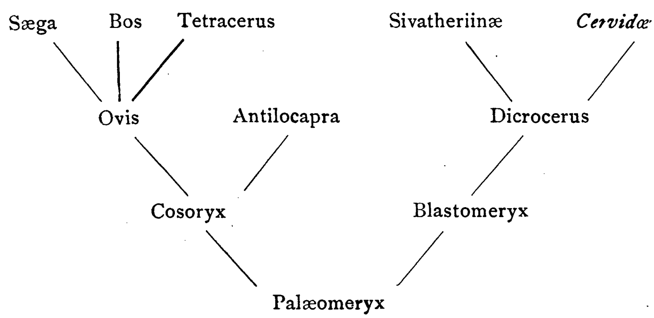
[4] In *Bos americanus* the postzygapophyses are single except on the last lumbar.

[5] Die Rinder der Tertiär-Epoche; Abh. Schwieiz. Pal. Gess., v, 1878.

displays the parietal extremely reduced, and become chiefly lateral in position. As regards the forms of the horns themselves, they present no important differences, but are angular and revolute in the section Ovis, and cylindric in the division Antilope. In the latter they vary in direction from straight to spiral or curved in different directions. Within the genus Ovis the end of the muzzle is naked or hairy, the latter in the typical forms and in those inhabiting northern and alpine localities generally. Those species that inhabit grassy or desert plains have the end of the nose naked.

Within the genus Bos modifications are observed parallel to those in the genus Ovis. The frontal bones with the horn processes are produced more and more posteriorly until the parietal bones are reduced to a narrow band across the posterior part of the skull. The bisons have the horns most anterior ; then follow the buffalos, and the extreme is reached in the true oxen, of which the domesticated animal is the type.

The following table will give an idea of the phylogeny of the Bovidæ.



The hornless Palæomeryx has given origin to the horned Boöidea ; on the one hand to the brachyodont (Blastomeryx, etc.), and on the other to the hypsodonts (Cosoryx, etc.). A cornification of the integument in a fork horned Cosoryx produced Antilocapra, while the same process in a simple-horned Cosoryx, produced Ovis. The development of this type has undergone the three principal modifications indicated by the three genera which succeed upwards. In Sæga an extra-

ordinary development of the muzzle takes place, which causes a change in the relations of the nasal bones. In Tetracerus another pair of horns is developed in front of the usual pair. Bos developes complications of the molar teeth in both jaws.

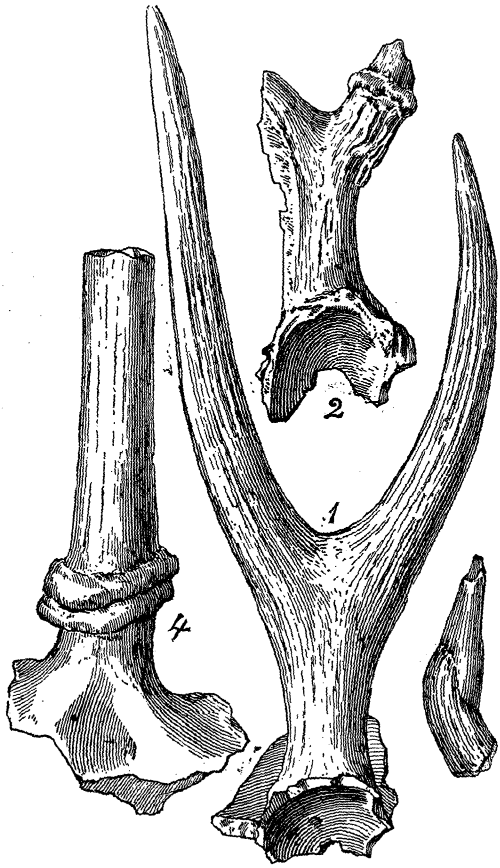


FIG. 18.—Cosoryx horns, three-quarters natural size, showing burrs and repaired fracture. Figs. 1-2, *C. necatus* Leidy. Figs. 3-4, *C ramosus* Cope. From the Loup Fork Miocene of New Mexico. From Report U. S. G. G. Surv. w. of 100 meridian.

On the brachyodont side the development of the dermal covering of the horns of Blastomeryx is arrested, and naked horned types follow. In the Sivatheriine group no further

change follows except complication of the horns. In the Cervine group, on the contrary, the habit of shedding them becomes fixed, and a new family has its origin.

No species certainly referable to Palæomeryx or Dicrocerus have been as yet found in North America, but they may be detected at any time. Numerous species have been found in Europe. Cosoryx is abundant in North America, six species being known (fig. 18, *C. necatus and C. ramosus*). They vary in size from that of a gazelle to that of a

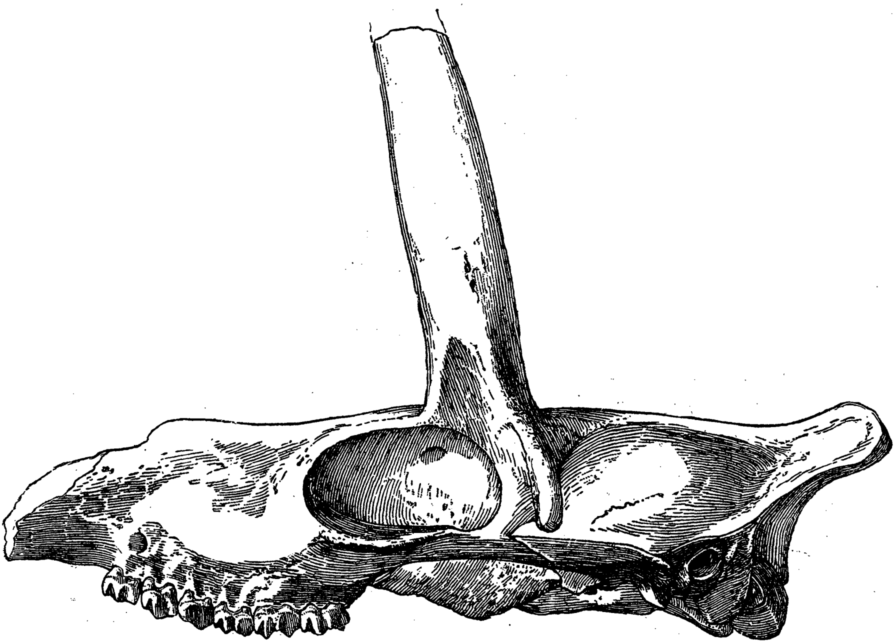


FIG. 19—*Blastomeryx borealis* Cope, one-sixth nat. size. From Ticholeptus bed of Montana; original.

fallow-deer. Although they did not shed their horns, some individuals developed a burr near the base of the beam, and burrs are found on the branches followed by broken down bone (Figs. 18, 2). In other cases broken points of antlers have become reattached, showing the presence of an integument to retain them. I have suggested that the development of the burr was due to the stripping or laceration of this integu-

ment to and at the base of the beam, producing an engorgement of the vessels and deposit of calcic phosphate; and that the stripping of the horns when complete resulted in their death and subsequent sloughing, thus originating the periodical shedding of the horns characteristic of the deer. This periodicity would depend on the periodicity of the season of reproduction, when the horns are especially used in conflicts between the males (Fig. 17).

Two species of Blastomeryx are known, a smaller, and a larger (*B. borealis*, Fig. 19), which was about the size of the Virginia deer. It is common in the beds of the Ticholeptus epoch. At the base of the horn on each side, a wing-like expansion extends outwards posterior to the orbit, giving a peculiar appearance to the anterior view.

The extinct species belonging to the Sivatheriinæ are only known from the upper Cænozoic beds of India, and they are among the most remarkable of the Artiodactyla. Several of them were of gigantic size, and their horns were of curious and formidable shapes. In the *Sivatherium giganteum* Cautl. Falc., the fore legs were longer than the hind legs; the forehead was concave, and furnished with a supraorbital horn on each side. The posterior horns were broadly palmate, and the muzzle is supposed to have been produced and convex above, as in the moose (Fig. 20).

The smaller Bovidæ are called Antelopes. Extinct species are numerous in the upper Cænozoic formations of Europe. and Asia, but they are wanting from corresponding beds in North America. The European species are related only subgenerically to those now existing in central and south Africa. All sorts of grada-

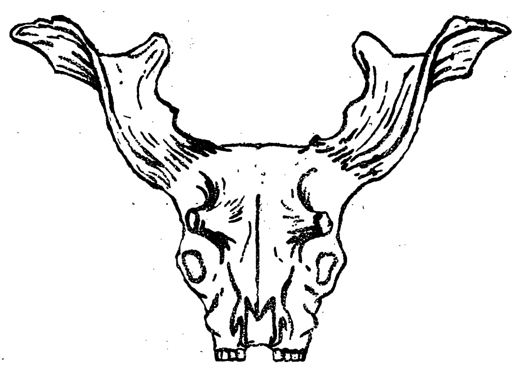
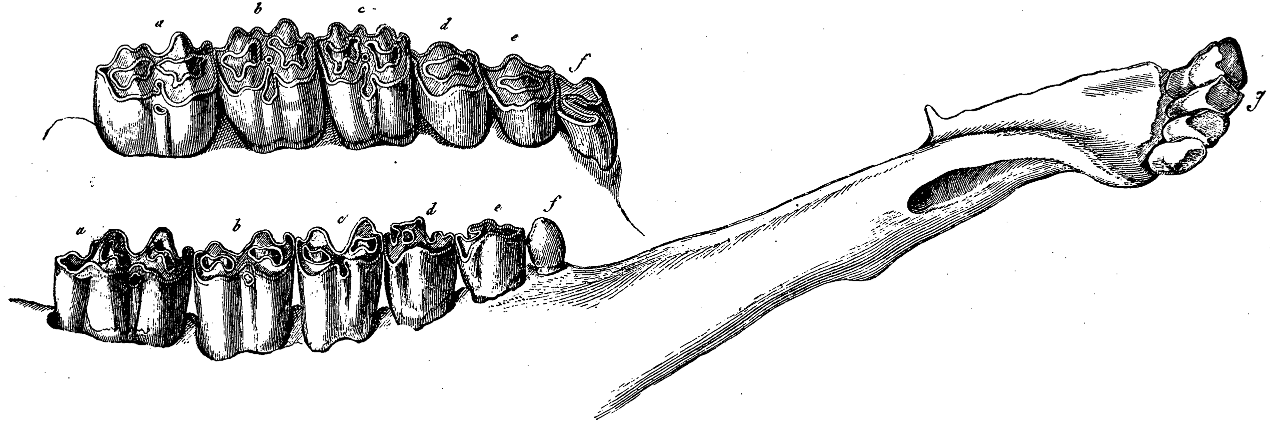


FIG. 20—*Sivatherium giganteum* C. F. cranium from front, much reduced. From Falconer. Miocene, India.

PLATE VII.



Bos taurus (from Cuvier.)

tions leading to the true genus Bos are found, especially in India, where many species of large size and various development of horns have been found. It appears that Bos is a polyphyletic genus, the divisions known as Bison, Bubalus and Bos, having arisen from as many types of Antelopes, which resemble them in the positions of the horns. In North America the division Bison only has been found, and this in Plistocene beds. Such are the species *Bos alleni* Marsh, and *B. latifrons* of Harlan. The latter species was of large size, the horn-cores of some specimens being as thick as a man's leg. It is evident that the line of the Boöidea was not continuous in North America, but that its later representatives were derived from the old world.

The following series may approximate a correct representation of the phylogeny of the genus Bos, expressed in genera.

Bos	
Ovis (sens. lat.)	Bovidæ.
Cosoryx	
Palæomeryx	
Dremotherium	Moschidæ.
Amphitragulus	
Gelocus	Tragulidæ.
Leptomeryx	
Dorcatherium	
*	
Anthracotherium	Anthracotheriidæ.
Cebochœrus	
*	
Pantolestes	Pantolestidæ.

Of the Cervidæ or the Boöidea which shed their horns, the genus Cervus is one of the earliest with which we are acquainted. Undoubted species of the genus occur in the Pliocene, and Upper Miocene species are also referred to it. As species from the Lower Pliocene (*C. matheroni* Gerv.) are referred to Capreolus, those of the Miocene may not be true Cervi. Their structure is not sufficiently known to determine this point. The arrangement of the genera is as follows. The three primary divisions were established by Brooke.

I Lateral metapodials complete only distally, and supporting dewclaws (Telemetcarpi).

a. Nasal passages posteriorly two, separated by vomer (Cariaci).

Horns simple spikes .... *Coassus* Gray.
Horns more or less furcate .... *Cariacus* Gray.
Horns palmate .... *Rangifer* H. Smith.

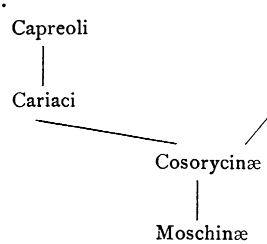
aa. Nasal passage posteriorly one, not divided (Capreoli).

No horns .... *Hydropotes* Swinh.
Horns furcate; no postantler .... *Capreolus* Gray.
Horns palmate; no postantler .... *Alces* H. Smith.
Horns palmate; a postantler .... *Cervalces* Scott.

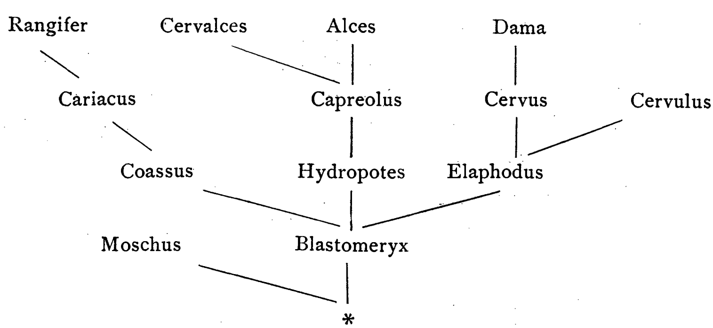
II. Lateral metapodials represented by proximal splints only; nasal passage not divided (Plesiometacarpi). (Cervi).

Frontal cutaneous glands; horns furcate .... *Cervulus* Blv.
No frontal glands; horns simple .... *Elaphodus* M. Edw
No frontal glands; horns furcate .... *Cervus* Linn.
No frontal glands; horns palmate .... *Dama* H. Smith.
Horns furcate; brow antler greatly exceeding beam, (Gill) ... *Elaphurus* M. Edw.

The phylogeny of these genera cannot be fully known until the skeletons of the extinct genera and species have been obtained. It is, however, certain that the short series of genera included in each of the three divisions (II *a* and *aa*, III) are genetic series; and also that division I is ancestral to both II and III, although perhaps by an extinct genus differing in some respects from Moschus. These relations can be thus expressed:



or thus:



Each of the genetic series commences with a genus with no or with very simple horns. The next genus or stage presents branched horns, sometimes of great complexity. The last term in each is the palmate horn, where a greater or less number of the tines unite to form a plate. These series, as is well known, correspond with the history of the growth of the horns in successive years of the life of each species. (Fig. 21.)

None of the genera of this family are extinct except Cervalces Scott.

The true Cervidæ form a family of very recent origin, and only distinguished at the period when forms like Cosoryx and Dicrocerus began to shed their horns. Dicrocerus is repre-

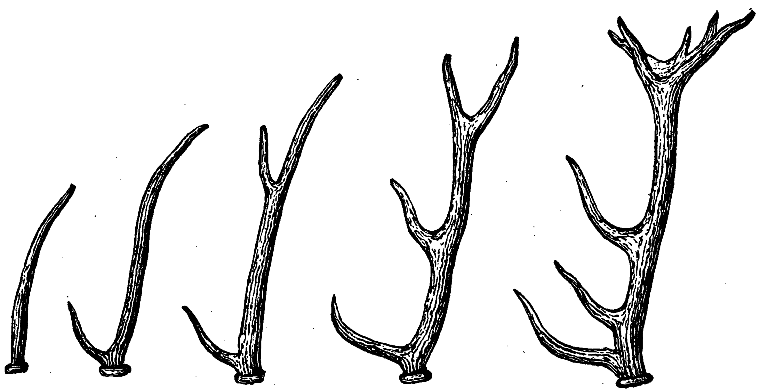


FIG. 21. Horns of *Cervus elaphus* from the second to the sixth years inclusive. From Cuvier.

sented by several species in the middle Miocene of Europe, and their horns are mostly bifurcate as in the third year's horn of a true deer. In the middle Miocene and part of the Pliocene the horns have three antlers as in the fourth year of Cervus, and as is permanent in the genus or section Rusa of tropical Asia.

The many branched horns appear in the Pliocene and Plistocene in Europe, in numerous species. In America extinct Cervidæ are more abundant than Bovidæ. Several species occur in the Pliocene beds of Buenos Ayres, and of Washington. The latter are related to the Moose (*Alces brevitrabalis* Cope) and American deer, (*Cariacus ensifer* Cope.) A very

remarkable species occurs in the Plistocene beds of the eastern region, the *Cervalces americanus* Harlan. Its affinities are with the Moose, with which it agrees nearly in size ; but it differs in possessing a posterior branch to the horn, which forms a broad, curved plate extending outwards above and behind the orbit, which resembles somewhat a hearing trumpet.

ADDENDUM.

In the first part of this article in the NATURALIST for December, 1888, p. 1088, I have given the characters of the sub-family, Dicotylinæ, of the family Hippopotamidæ, and of the two included genera, Dicotyles and Platygonus. Some amendment of these definitions is necessary, as follows: That of the sub-family "Digits three" should be supplemented by the words,—on the anterior foot, and four on the posterior. The genera are both stated to have premolar teeth similar to the true molars. This statement must be qualified as regards the species now referred to Dicotyles, and must be contradicted as regards Platygonus. In the latter genus the deciduous premolars only resemble the true molars (fig. 6, p. 1093), and they have the peculiarity of remaining in the jaw until the last true molar is nearly protruded. In Dicotyles, the deciduous teeth have disappeared before the last true molar is protruded. The permanent premolars are, as Leidy has described them, generally simpler than the true molars, consisting of two external, and one internal tubercle.

But the species differ so much in the characters of their premolars that they can be referred to three subdivisions, which may be at some future time regarded as genera. These are as follows:

I. Premolars all different from molars (*Notophorus* Gray) ; *D. tajassus*.

II. Last premolar only, like the molars (*Dicotyles* Cuv.) ; *D. labiatus* Cuv. ; *D. serus* Cope ; *D. angulatus* Cope.[1]

III. Second premolar (from front) like true molars (*Mylohyus* Cope) ; *D. nasutus* Leidy.

It is uncertain whether the complex premolar of *D. nasutus*

[1] AMERICAN NATURALIST, Feb. 1889.

is the penultimate or the last premolar. If it is the last, the genus Mylohyus will be distinguished by the presence of only two premolars.

An examination of the crania of *Dicotyles tajassus* in the U. S. National Museum from Costa Rica, shows that they display characters intermediate between the Brazilian typical form, and the *D. angulatus* of Texas. The last premolar teeth are sometimes premolariform, and less frequently approach the molariform structure. The facial angle is continued to the position of the canine aveolus, and the ridge of the maxillary bone is only separated from its border by a groove, not a fossa. The nasal bones are not tectiform. In general the characters agree with the *D. tajassus*, but the lateral facial angle is as in *D. angulatus*, and occasionally the last premolar resembles that of the same species. It appears then that the latter must be regarded as a subspecies rather than a species.

EXPLANATION OF PLATES.

PLATE III.

Agriochœr s guyotianus Cope, skull, natural size; from side, and one-half from below. From the John Day Bed of Oregon. Original from unpublished plate in Report of U.S. Geol. Survey Terrs.

PLATE IV.

The elbow joint of Mammalia, separated, and seen from above and posteriorly. A, *Crocuta maculata.* B, *Simia nigra.* C, *Rhinolophus* sp. D, *Eucrotaphus pacificus.* E, *Cervus elaphus.* All four-fifths natural size.

PLATE V.

Vertebræ of Artiodactyla, two-thirds natural size. Fig. 1 *Antilocapra americana;* 2, *Dicotyles angulatus;* 3, *Capra hircus.* *Prz* prezygapoplysis; *Poz* postzygapoplysis; E.S. Episphen.

PLATE VI.

Hypertragulus calcaratus Cope, skull, natural size ; from the lower Miocene. Fig. 1, lower jaw from above, of specimen from White River bed of Colorado. Fig. 2, skull from John Day series of Oregon ; *a*, side, *b*, from above, *c*, from below.

PLATE VII.

Bos taurus, dentition, two-thirds natural size ; from Cuvier.

EDITOR'S TABLE.

EDITORS E. D. COPE, AND J. S. KINGSLEY.

The position of the Post-Darwinians is clearly set forth in an abstract of a lecture delivered by Prof. E. Ray Lankester, at the London Institution, which appears in *Nature* of February, 28th. Prof. Lankester declares that the error of Lamarck (and consequently of the Neolamarckians,) consists in the assumption that acquired characters can be inherited. He says, "Congenital variation is an admitted and demonstrable fact; transmission of congenital variations is also an admitted and demonstrable fact. Change of structure acquired during life—as stated by Lamarck—is also a fact, though very limited. But the transmission of these latter changes to offspring is not proved experimentally ; all experiment tends to prove that they cannot be transmitted." Two inferences may be derived from these statements. First ; the author of them does not believe that the so-called congenital variations can be or have been acquired ; second ; that he has no hypothesis to offer in explanation of the origin of congenital variations. These positions exclude another inference which nevertheless may be derived from other propositions embraced in the abstract of the lecture. He says, with Lamarck, that "change of structure acquired during life is also a fact," and also that "all plants and animals produce offspring which resemble their parents on the